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XIV.—*On Recurrent Animal Form, and its Significance in Systematic Zoology.* By CUTHBERT COLLINGWOOD, M.B., F.L.S., &c.*

No ONE conversant with Zoology can have failed to remark the fact of the recurrence of similar forms in different groups of the animal series. Not only do species of one family resemble species of an allied family, but group with group, order with order, and even class with class, and subkingdom with subkingdom, can produce instances of the most striking homomorphism. The resemblances to which I allude are those of external form, unaccompanied by homologies of internal structure; nevertheless I imagine that this peculiarity, instead of entirely destroying its interest, and rendering it valueless, as some have appeared to consider, only places the subject in a different category of scientific facts, and invests it with a value peculiar to itself. In the history of classification it has always naturally happened that external form, rather than internal structure, has been the main-spring of systems; the knowledge of structural homologies has been painfully accumulated, and the systems built upon the characters presented by external form have from time to time been corrected by increasing knowledge of structure, till in these days zoologists have agreed that *structure*, and not *form*, should be the basis upon which systems should be framed with the greatest claim to accordance with Nature. Nevertheless systems founded upon *homologies* are liable to be interfered with, and their symmetry affected by encroachments of form; so that eminent zoologists differ as to the position of animals, even in the present advanced state of zoology, owing to the fact that, while one regards *homologies of structure* as paramount, another allows

* Communicated by the Author, having been read before the British Association at its Meeting at Oxford (1860).

great weight to external and striking *resemblances in form*. Under these circumstances, therefore, it can be no waste of time to inquire what connexion exists between the two, and to attempt to point out a cause for *agreements of form*, in cases where corresponding *agreement in structure* is wanting.

Nature is inexhaustible in resources; and variety is one of her greatest charms. It is often said that no two things in Nature are alike, and with truth; for the resemblance, whether in outward form, or in internal organization, always partakes of the character of a *near approach*, and not of *distinct repetition*. This is particularly the case with *form*, which varies more, and is more simple in its variations than structure; and it is this which confirms my belief that *structure*, and not *form*, is at once the truest basis of Systems of Nature, and the safest criterion in cases of doubt and difficulty. Thus, an Archetypal animal may agree to a certain extent in *structure* with a vast group of animals, and yet may resemble none of them in outward *form*.

It cannot be a matter of surprise, considering the number of such resemblances existing throughout the animal kingdom, that while the study of homologies was making but slow progress, and the true affinities of animals were but little understood, the real nature of many aberrant forms should have been lost sight of in the contemplation of their homomorphic resemblances. Who can wonder if Pliny spoke of the Bat as "the onely bird that suckleth her little ones," in quaint old Holland's phraseology? What malacologist even can feel surprise that, up to recent times, the Polyzoan Molluscoids were mistaken for Zoophytes? or that Lhuyd, and at one time the illustrious Ellis, should have regarded them both in the light of "remarkable sea-plants," while his predecessor, Baker, had even looked upon them as the production of "salts incorporated with stony matter"? Who can wonder that, before the time of Savigny, the Tunicated *Botrylli* should have been regarded as Polypes? that Linnæus should have placed *Teredo* among the Annelides? that, before the Mémoire of Dujardin in 1835, the Foraminifera should have been classed with the Cephalopodous Mollusca? In all these cases (and others might be brought to swell the list), the animals have been raised, or have sunk, from one *subkingdom* to another.

But, although they were not always recognized as such, the existence of recurrent forms in Nature could not be overlooked by the framers of systems, inasmuch as they were stumbling-blocks, which almost seemed placed in their path to prevent the natural arrangement of animals from being too easy a task. A too cursory examination has not unfrequently resulted in the false location of an animal, only to be detected, and triumphantly exposed, by a succeeding zoologist.

Every one knows, whether he have thought about it or otherwise, that the four Vertebrate classes are homomorphically connected. Thus there are Flying Mammals, such as the Bats and Flying Squirrels (*Pteromys*), uniting them with the Class Aves; as well as that anomalous Monotreme, the *Ornithorhynchus*, or Web-footed Duck-bill. The Edentata among Quadrupeds connect them with Reptiles, by means of the Armadillos,—the Great Armadillo (*Dasypus gigas*), and preeminently the Mataco (*D. Apar*), being homomorphic of the Testudinata, while to the Saurian Reptiles they are united by the Scaly Pangolins (*Manis*), and to the extinct Pterosaurians (Pterodactyles), again, they are united by the Bats. With Fishes, the Mammalia are most singularly connected by the Cetacea; while a special resemblance appears between the Narwhal (*Monodon*) and the Swordfish (*Xiphias*).

The homomorphic resemblances between Birds and Reptiles are not striking; but the Draconine Saurians or Flying Lizards (*Draconis*, sp.) supply examples, and the extinct Pterodactyl once afforded another; while with Fishes the various species of Flying-fish (*Exocoetus*) among the soft-finned, and Flying Gurnards (*Dactylopterus* and *Pterois*) among the hard-finned, are good illustrations. It only remains to connect Reptilian forms with Fishes; and here the Snakes (*Ophidia*) may well be compared with the Eels; and less striking instances of resemblance occur between the Saurian reptiles, such as the Alligator, and the bony-cased Sturgeon, and between the Testudinata and the Trunk Fishes (*Ostracion*). Perhaps also that great Enaliosaur the Ichthyosaurus might be here mentioned.

Without extending my illustrations too far, I will select the Mammalia as an example of the recurrence of form within the limits of a single Class. The organic structure and affinities of one *Order* are dissimilar from those of another, just as the structure and affinities of one *Class* differ from those of another; the difference between Class and Order being one of *degree*, and not of *kind*; so that it is as remarkable to find resemblances of form in widely separated *Orders* as in still more widely separated *Classes*, although, of course, homomorphic resemblances are more striking between Orders than between Classes. In the Order Quadrumana, for instance, we shall find representative forms of various other Orders. Thus the genera *Midas* and *Iacchus*, known as Marmozets, true Platyrrhine Quadrumana, represent the Rodentia through the genus *Sciurus* (Squirrel); and the Douroucouli (*Nyctipithecus felinus*), in the same division, represents the Cat (*Felis*) in the Digitigrade Carnivora; while, among the Strepsirrhine Quadrumana, the Loris (*Stenops tardigradus*) represents the true Sloths in the Order Bruta, and the very

aberrant animal, falsely called the Flying Squirrel (*Galeopithecus*), is the representative of the Order Cheiroptera, or Bats.

Among the Pachydermata are some no less striking examples of species homomorphic with those of other Orders. Thus the Hyrax, an animal in structure intermediate between the Rhinoceros and Tapir, a miniature Rhinoceros, as it has been called, yet so closely resembles the Rodentia in its outward form, that it was long classed with them; and Cuvier makes the following remark concerning it:—"There is no quadruped," he says, "which proves more forcibly than the Daman (*Hyrax capensis*) the necessity of having recourse to anatomy as a test by which to determine the true relationship of animals."

The general resemblance between the Cetacea and the Pinnigrade Carnivora (Seals) need only be referred to; it is made very distinct through the herbivorous family Manatidæ, especially the Dugong (*Halicore Dugong*).

We have seen how the Loris resembles the Sloth; and on the other hand, the Edentate genus *Bradypus* (Ai) bears a singular resemblance to Monkeys in general, even in that particular which is so characteristic of them, viz. their physiognomy, while it has a carnivorous homomorph in the Sloth Bear (*Ursus labiatus*), called by Pennant the Ursiform Sloth, and by Shaw, *Bradypus ursinus*.

The Insectivora are connected through the Hedgehog (*Eri-naceus europæus*) with one of the most anomalous of animals, the singular Monotreme genus *Echidna*, which has, besides, other homomorphs, to be afterwards mentioned; and further through the Shrews (*Soricidæ*), with the Rodent genus *Mus*; and with the Carnivora by the Bulau (*Gymnura Rafflesii*), formerly described as a Viverra.

The Rodentia are united homomorphically with the Pachydermata by means of the Capybara (*Hydrochærus Capybara*), formerly called, from its pig-like appearance, *Porcus fluviatilis* (Fermin), Thick-nosed Tapir (Pennant), Cochon d'eau (Desmarchais), and *Sus maximus palustris* (Barrère). By the Flying Squirrel (*Pteromys*) they claim some homomorphic affinity with the Cheiroptera; but their chief homomorphism is with the Marsupialia, and most striking are the resemblances. Not only do the Rodentia and Marsupialia bear a general mutual resemblance throughout, both Orders possessing that extraordinary development of the hinder extremities and tail which enables the Jerboas, in common with Kangaroos, to take such wonderful leaps, but there are particular animals in both Orders which bear a most remarkable resemblance to one another. Thus, the Rodent Jerboas (*Dipus*) are closely imitated by the Tufted-tailed Rat-Kangaroo (*Hypsiprymnus penicillatus*,

Gould); and the true Kangaroos (*Macropus*) are equally nearly approached in form by the Cape Leaping Hare (*Pedetes capensis*, Ill.). There is also a considerable resemblance between the Wombat or Badger of the Australian colonists (*Phascolomys Wombat*, Pér. and Les.) and the Rodent Cavies and *Lagomys*; while a further homomorphism occurs between individuals belonging to aberrant groups in either Order, viz. the Brazilian Porcupine (*Syntheres*) among the Rodents, and the Echidna among the Monotremes, whose relation to the Insectivora has already been pointed out.

These external resemblances between Rodents and Marsupials are none the less remarkable when we learn that there is less true affinity between them than between the Marsupials and most other Orders; for Mr. Waterhouse, in his excellent 'History of the Marsupialia,' remarks that in them "we find representatives of most of the other Orders of Mammalia. The Quadrumana are represented by the Phalangera; the Carnivora by the Dasyuri; the Insectivora by the small Phascogales; the Ruminantia by the Kangaroos, and the Edentata by the Monotremes." He adds: "The Cheiroptera are not represented by any known Marsupial animals, and the Rodents are represented by a *single species only*"—the species referred to being the Wombat.

Lastly, the Marsupialia, besides their homomorphism with the Rodents, have, through the Ursine Opossum, or Native Devil of Van Diemen's Land (*Dasyurus*), a singular relationship to the Carnivorous genus *Ursus*, as well as, through the Squirrel Petaurus, to the Bats.

Space will not permit me to compare the forms of Invertebrata one with another. Among them many remarkable analogies of form may be observed; and even between the Vertebrata and Invertebrata they will be found to occur. Further illustrations of this subject may be found in a paper by the author in the 'Proceedings' of the Liverpool Literary and Philosophical Society for the past session.

On no principle of gradation of *form* can these resemblances, unaccompanied as they are by homologous relations, be accounted for. Some are *advances*, others *degradations* of form; and we must look for some deeper and more subtle cause which shall connect animals so widely separated as are the members of distinct subkingdoms. There is one circumstance, however, which cannot fail to strike the thoughtful inquirer, and which, I think, holds out a clue to the remarkable facts to which I have just now briefly alluded. The circumstance to which I refer is, that, in not a few cases, striking deviations from typical *form* are accompanied by no less striking modifications of typical *habits*; and further, that these *modified* habits have a strong

tendency to assimilate with the habits naturally exhibited by those animals whose form they assume. It is not easy to compare the habits of animals essentially different in structure, and occupying widely separated positions in the animal kingdom; but a few examples taken from within a Class will illustrate my meaning, and give us an opportunity of carrying the arrangement forward to cases of greater complexity. Thus, the Ursine Opossum (*Dasyurus ursinus*), widely separated as it is from the Plantigrade Carnivora, not only agrees far more closely with a Bear in form than with its own congeners, having a short clumsy figure and Plantigrade step, but it is said of them, by their discoverers, that "they frequently sat on their hind parts, and used their fore paws to convey food to their mouths, and many of their actions, as well as their gait, strikingly resembled those of a Bear*."

The Quadrumanous Douroucouli (*Nyctipithecus felinus*) not only resembles a Cat in form, but is, like it, nocturnal in its habits, glides about with the stealthy movements of a cat, and "when irritated, in the posture it assumes, and the puffed state of the fur, it resembles a cat attacked by a dog." The pachydermatous Hyrax lives gregariously in burrows, like the Rabbits, which it so closely resembles in form. The Echidna rolls itself up into a ball when disturbed, like its homomorph the Hedgehog; the Lemurine *Galeopithecus* makes its flight with its young attached to the nipple, as do the true Bats. The habits and food of the Sea Eagle closely agree with those of the Albatros; and the Burrowing Owl is diurnal in its habits, and uses its feet more or less for purposes of scratching, in both which respects it differs from its congeners, and agrees with the Rascals, which it resembles in form.

In all these cases—and the list might be greatly swelled—the agreement between form and habit, independent of homological relations, is so striking that one is almost led to the conclusion that a certain external configuration necessitated certain habitual movements. I do not mean to say that this is the case; but I am inclined to think that a more careful review will lead us to the conviction that the converse of this proposition is the secret, not only of these, but of the other striking cases of *homomorphism*, as it has been called, to which reference has already been made.

The principle may be thus stated:—*That agreement of habit in widely-separated groups is accompanied by similarity of form.* Let us now see if we are not justified in deriving such a principle from instances such as those just adduced, added to what knowledge we possess with regard to the habits of animals in

* G. P. Harris, in Linn. Trans. ix. p. 174.

general; and commencing with cases of the greatest simplicity, let us pass on to those which are more complex.

Now, among all the Vertebrate Classes there are certain general homologies which structurally unite every animal contained within them, however it may differ in external form. In all, the diverging appendages are present in some form or other, except, indeed, in certain Ophidians, in which they are entirely absent. In Birds, the modification of the fore extremity is obvious, and in Fishes only somewhat less so; but, although the relative position of the pectoral and ventral fins is sometimes reversed (as in the Perch, for example), still the pectorals are *always* homologous with the fore, and the ventral with the hind limbs of other Vertebrata. There is therefore a great community of *plan* in Vertebrates, with respect to those parts which constitute the elements of external form.

Let us now glance at the media in which they move. Mammalia are, as a class, destined to tread the surface of the earth, birds to fly in the air, and fishes to swim in the sea: but neither is the air nor the sea devoid of Mammalian inhabitants; and both land and water, as well as air, afford a home for birds. Reptiles also occupy all three stations; and fishes alone, being essentially water-breathing animals, as well as of a decidedly inferior grade of organization, never quit that element. But in order that a mammal may be adapted to an aquatic existence, it must be fashioned more or less in the form of a fish; an elaborate hand or foot would be useless, and projecting appendages injurious. It is therefore piscine in form, covered with a smooth skin, and differs from a fish only in the position of the tail, which, being horizontal instead of vertical, is an index of its air-breathing habits. So also an aquatic bird has a smooth covering of close-set feathers, an attenuated head, fin-like wings, and feet situated so far back as to answer the purpose of a propelling tail when in the water; and could we see a Penguin in the act of swimming beneath the waves, it would undoubtedly have the aspect of a fish. Take, again, the Seals, in which these aquatic habits are not so complete as in the Cetaceans, and we find them modified in form to be something intermediate between a fish and a mammal; while an Otter, which is rather terrestrial than aquatic, has its quadrupedal character still less modified: in it we find the close-set fur, the depressed form, and the webbed feet; but the feet are not fins, nor is the tail.

With regard to flying quadrupeds, it is of course more or less necessary that the upper extremity should form a wing of some kind, which, however different in the homologies of its parts from the wing of a bird, must necessarily bear some general resemblance to it in form. A Bat is as purely an aerial animal as is a

bird ; but its wing, not being formed upon the type of that which exists in a true bird, must be inferior ; nevertheless it is as truly and completely a wing as is the far more perfect, but less bulky, wing of a bird.

Further, if we select a single Class, such as the Mammalia, and bear in mind the same principle, we shall find it lead to the same results. Some quadrupeds of each Order are arboreal, some terrestrial, and others subterranean ; some are carnivorous, some insectivorous, and some frugivorous ; some are nocturnal, some diurnal, and some crepuscular. If, now, an animal belonging to one Order is, like an animal of a different Order, insectivorous, the former probably bears some remote analogy to the latter, by virtue of that fact. If the animals of two different Orders are not only *both* insectivorous, but also crepuscular, for example, the probability of their resemblance is increased ; but if the two are insectivorous, crepuscular, *and* subterranean, then the great agreement of their habits must be accompanied by a considerable approximation of form.

Perhaps there are no facts in the natural history of animals which are simpler, or with which we are more familiarly acquainted in a general way, than the broad characteristics which differentiate the habits and modes of life of quadrupeds, birds, and fishes ; and, on the other hand, the aberrant forms which are assumed by aquatic mammals and birds, and by aerial quadrupeds, and the homomorphism of these aberrant forms with those of the classes of Vertebrata which they most nearly approach in their habits and modes of life, are highly important questions, which thus admit of elucidation with a degree of probability commensurate with this exactness of our knowledge of those habits. The kind of homomorphism which obtains between members of a Class, such as among the various Orders of the Mammalia, requires a different kind of knowledge, viz. not a general acquaintance with broad facts, but a special familiarity with individual habits. Now, such a special knowledge is by no means always possessed, or even easily attainable ; but when it is so, it is found that the greater the agreement of habit and modes of life between any two animals of distinct Orders, the more striking is the homomorphism which exists between them. Of this proposition several illustrations have already been given.

Taking now our stand upon these facts, and carrying the principle which I have laid down into the Invertebrate division of animals, the first thing which strikes us is the comparative artificiality of some of the resemblances which might be instanced as existing between them and the Vertebrate subkingdom. The habits of a Mollusc and a Fish can scarcely be compared ; still less can those of a Tunicate and a Reptile, or of an Infusory

and a Quadruped, and yet we perceive between them close resemblances of form ; but between a Worm and a *Siphonops*, or between an Insect and a Bird, we can readily argue a community, because we at once estimate the narrow limits in the one case, and the wide extent in the other, of their analogical functions. It would be highly unphilosophical to suppose that these close resemblances were the effect of accident, and still more so to say that they result from accident in one case, and from profound design in another.

The homomorphisms existing between the Vertebrata and Invertebrata are not numerous ; indeed, as might be expected in animals so widely separated, they are rare, and usually imperfect. I confess they present the greatest difficulty ; and yet, where knowledge of habit assists us, the difficulty to a great extent vanishes. There is no Class of Invertebrata more familiarly known than the insects, and there are no clearer homomorphisms between these great subkingdoms than those between insects and birds ; and who is there that does not perceive that the forms assumed by insects are as much the necessity of their habits, and that in habits, as in form, they assimilate to birds, just as a Bat does, or as a Whale agrees with a fish.

Again, how little do we know of the habits of the Invertebrate classes generally ? The majority of them are marine ; and it is only quite recently that they have even been *seen*, except through the medium of pictures, by the majority of persons. We are not on terms of familiarity with *them*, as we are with quadrupeds and birds ; and seeing that our comprehension of their homomorphism is in direct ratio to our knowledge of their habits and modes of life, it is not a matter of surprise that we should be unable to penetrate the mystery of the similarity between the Foraminifera and the Mollusca, or between the Polypes and the Polypine Infusories. For here again the explanation of their homomorphism is measured by the amount of our knowledge. We see why a *Bombylius* resembles a *Bombus*, or a *Teredo* a *Sabella*, having some acquaintance with the similar habits of each, and seeing a degree of similarity between them. We know why a Caddis-worm resembles a Tubicolous Annelide, and this, again, a tube-inhabiting Rotifer ; it is the common habit of forming a tube for their otherwise unprotected body which assimilates them ; but we know not why a *Chiton* resembles an *Aphrodite*, because we are equally ignorant of the habits of either.

Let me now, in application of the foregoing principles, throw out some suggestions in relation to the most striking instance of homomorphism which occurs, perhaps, in the animal kingdom—viz. that existing between the Polyzoan Molluscoids and the Hydroid Polypes. In both these widely-separated groups, we

have certain compound forms made up of numerous membranous or calcareous cells, upon a common axis or stem, which branches in a plant-like manner, each cell being the habitation of a distinct animal. These are their homomorphic characters; now let me state what are the special characters of each group. First, Hydroid Polypes: mouth with filiform, simple tentacula; stomach excavated in the cellular substance of the body; no distinct muscular apparatus; body contractile in all its parts, gemmiparous externally. Secondly, Polyzoa: body not contractile, symmetrical; mouth and anus separate; gemmiparous and oviparous. It therefore appears that the Polyzoa are minute Molluscs, differing in all their homologies from Polypes. Let us next inquire of which group the Polyzoary form is typical. Clearly not of the Mollusca, which are for the most part of very different form; and equally clearly it is typical of the Polypes, in which Class it assists their analogy with vegetable forms. The Polyzoary form, then, is aberrant from the Molluscan, and typical of the Hydroid Polypes. Why this form is best adapted for the life of Polypes I am not required to prove, but only why (that being granted) it is also the best form for the Polyzoa. Next, let us inquire what differences exist in the form of the animals themselves. In the Polype there is a gelatinous substance hollowed out into a stomach, a single aperture serving the purposes of taking in food, and passing out rejectamenta and ova, this common outlet being surrounded with a circler of gelatinous contractile tentacles, armed with nettling capsules. But the Molluscoid has an œsophagus, stomach, gizzard, intestine, distinct anus, besides a liver and nervous system. In none of these particulars has it any relationship with Polypes; *but* the mouth is surrounded with a circler of tentacles, not indeed like those of Polypes, simple and contractile, but uncontractile, and covered with vibratile cilia. They are probably the homologues of the labial palpi of other Molluscs. This circler of tentacles then is the *great point of resemblance* between Molluscoids and Polypes—in the latter the common arrangement, in the former arising, as it were, from an accident or variety of organization; and yet is it not easy to perceive that the common possession of tentacles exhibited by Polypes and Polyzoa implies a very great similarity, nay, almost *identity*, in one of the most important of habits, namely the mode of procuring food?

Having so far established a community of habit between them, let us next refer to the grand organic distinction which is implied in the widely different form of the digestive apparatus. In the Polypes, the rejectamenta being passed out by the mouth, such animals are well fitted doubtless for living in cells with a single aperture; the Mollusca, however, have an intestinal canal,

